PALEOSCENE #9. Taphonomic Processes: Information Loss and Information Gain

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Introduction

The term "taphonomy" was coined by Efremov in 1940 to mean "the science of the laws of burial". The field unites aspects of paleoecology and sedimentology, and is of interest to paleoecologists, evolutionary biologists, biostratigraphers, systematists, and sedimentologists.

This paper begins by summarizing the history of taphonomy, different viewpoints regarding the definition and boundaries of the field, and taphonomic methods.

Two contrasting approaches to the application of taphonomy to specific problems are presented. The first and most popular approach is based on the assumption that biases (differences between the preserved fossil record and the recent community) and other effects of death and burial interfere with research goals. Five major research goals, both actual and potential, are identified and described for this first approach: (1) the reconstruction of ancient communities; (2) the reconstruction of the geometry of evolution; (3) the reconstruction of population characteristics; (4) biostratigraphic correlation; and (5) systematics. The second approach, more fashionable recently, is based on the observation that biases and other effects of death and burial can actually further certain research goals, particularly the reconstruction of ancient environments, if the focus is on the taphonomic processes. The two views of taphonomic processes, as causes of bias, incompleteness, and mixing on the one hand, and as sources of new insights into sedimentary geology and paleontology on the other, are referred to in the present essay as "taphonomic loss" and "taphonomic gain", respectively.

The assumptions of taphonomy are considered with respect to how they can be made most reliable, and with respect to how the loss and gain approaches can be complementary.

The question of whether there are universally applicable laws or generalizations in taphonomy is also addressed.

Throughout, a critical review is made of opinions in the field of taphonomy, and the viewpoint of the author is given. In order to keep the volume of information in this review manageable, some subjects (*e.g.*, ichnology and zooarcheology) for which taphonomic analysis is widely appreciated are not discussed.

History of Taphonomy

The great majority of taphonomic studies have been done very recently, and at present the field is one of the most active in paleontology. For example, at the North American Paleontological Convention at Boulder, Colorado, in August of 1986, 33 of 282 papers presented (12%) had a major taphonomic focus. An extensive summary of taphonomy with numerous examples is found in Müller (1979), and recent texts on paleontology and paleoecology devote considerable space to it (Dodd and Stanton, 1981; Gall, 1983). Several authors have recently summarized the history of the subject (Dodson, 1980; Olson, 1980; Behrensmeyer and Kidwell, 1985). Therefore, I will present only a brief historical review here.

Taphonomy has developed primarily on two continents, Europe and North America. In the first two-thirds of this century the German school of "aktuopalaeontology" (usefully summarized by Schäfer, 1972) was the most significant precursor of modern taphonomic investigation. More recently, Seilacher (1970) and colleagues (Seilacher *et al.*, 1976) have contributed through intensive analysis and reconstruction of unusual deposits (called "Fossil-Lagerstätten") of well-preserved fossils. An important parallel contribution was the concept of "event stratigraphy", in which each layer of sediment is looked upon as a unique and informative event (Einsele and Seilacher, 1982).

In North America, taphonomy grew out of paleoecology, developing somewhat independently along several different, taxonomically specialized lines (Olson, 1980). For example, in paleoecology of vertebrates an early goal was to reconstruct fossil communities by distinguishing between transported and untransported specimens, based on skeletal completeness (Shotwell, 1955). Although some of its effects were delayed, Shotwell's paper was followed by a great deal of work on sources of bias in fossil vertebrate assemblages (*e.g.*, Clark *et al.*, 1967; Olson, 1957; Voorhies, 1969). At about the same time, invertebrate paleoecologists were interested in interpretation of size-frequency distributions (Boucot, 1953; Johnson, 1960; Rigby, 1958), and distinguishing among transported *versus* untransported, and slowly- *versus* rapidly-buried death assemblages (Boucot *et al.*, 1958; Johnson, 1957, 1960). An important early work on aquatic vertebrates was that

by Zangerl and Richardson (1963).

More recently in North America there has been increased emphasis on comparisons between fossil and modern assemblages. Examples are Behrensmeyer's (1975) work with African mammals, Spicer's (1981) study of plant macrofossil deposition in a lacustrine delta, and the work of Lawrence (1968) on oysters. Another profitable area has been comparative studies of closely related taxa across different formations and paleoenvironments (Behrensmeyer and Kidwell, 1985). Examples using vertebrates are the studies of Dodson (1971) on the Cretaceous dinosaurs of Alberta, and Dodson *et al.* (1980a, 1980b) on Jurassic and Cretaceous dinosaurs of the western United States. An invertebrate example is the study of trilobite deposits by Speyer (1987). Taphonomic characteristics of three very different groups of lacustrine fossils (plant macrofossils, adult insects, and fish) have also been compared across numerous Eocene formations in British Columbia and Washington State (Wilson, 1980, 1982, 1988). The comparative approach has been summarized by Brett and Baird (1986) and has been characterized by Speyer and Brett (1986) in their study of Devonian trilobites, and in a more general study by the same authors (1988), as the search for "taphofacies", *i.e.*, facies defined by taphonomic traits.

The history summarized above is largely a history of the taphonomic-loss approach. The taphonomic-gain approach is newer, having been explored primarily by Elder and Smith (1984), Elder (1985), Behrensmeyer and Kidwell (1985), and Brett and Baird (1986).

Definition and Boundaries of Taphonomy

Viewpoints differ regarding the definition and scope of taphonomy. To some, taphonomy refers primarily to the study of the processes between death and burial of an organism, including cause and manner of death, decay, decomposition, transportation, and burial (Dodson, 1980). Efremov's (1940, 1950) original definition was broader, for it included fossil diagenesis and continent-scale biases in fossil preservation associated with sediment volume and outcrop areas. Valentine (1973) included all events between death of the organism and discovery of its fossils within taphonomy. Behrensmeyer and Kidwell (1985) preferred an even broader definition: "the study of processes of preservation and how they affect information in the fossil record". They argued that taphonomic methods could profitably be applied to both *pre*-death and *post*-burial circumstances. They emphasize that aspects of paleoecology such as species distributions, together with geologic factors such as diagenesis, tectonics, erosion, and outcrop patterns, influence and bias what we see in the fossil record.

On the whole, the boundaries of taphonomy can be conveniently left at death on the

one hand, including its immediate causes, and diagenesis on the other. A useful treatment is to divide the subject into three areas: "necrolysis", the death and decomposition of the organism; "biostratinomy", the sedimentary history of the fossil until burial; and "fossil diagenesis", the chemical and mechanical alteration of fossils within sediment (Dodd and Stanton, 1981). Some authors include necrolysis within biostratinomy (Müller, 1979), whereas necrolytic processes can in some circumstances occur simultaneously with early diagenesis. Normally, however, necrolysis precedes and partly overlaps with biostratinomy, which precedes diagenesis. Paleoecologic factors that are not directly involved in the cause and manner of death of the organisms, together with all post-diagenetic biases numerous as they are, are outside the scope of taphonomy *per se*, even though these fields share many
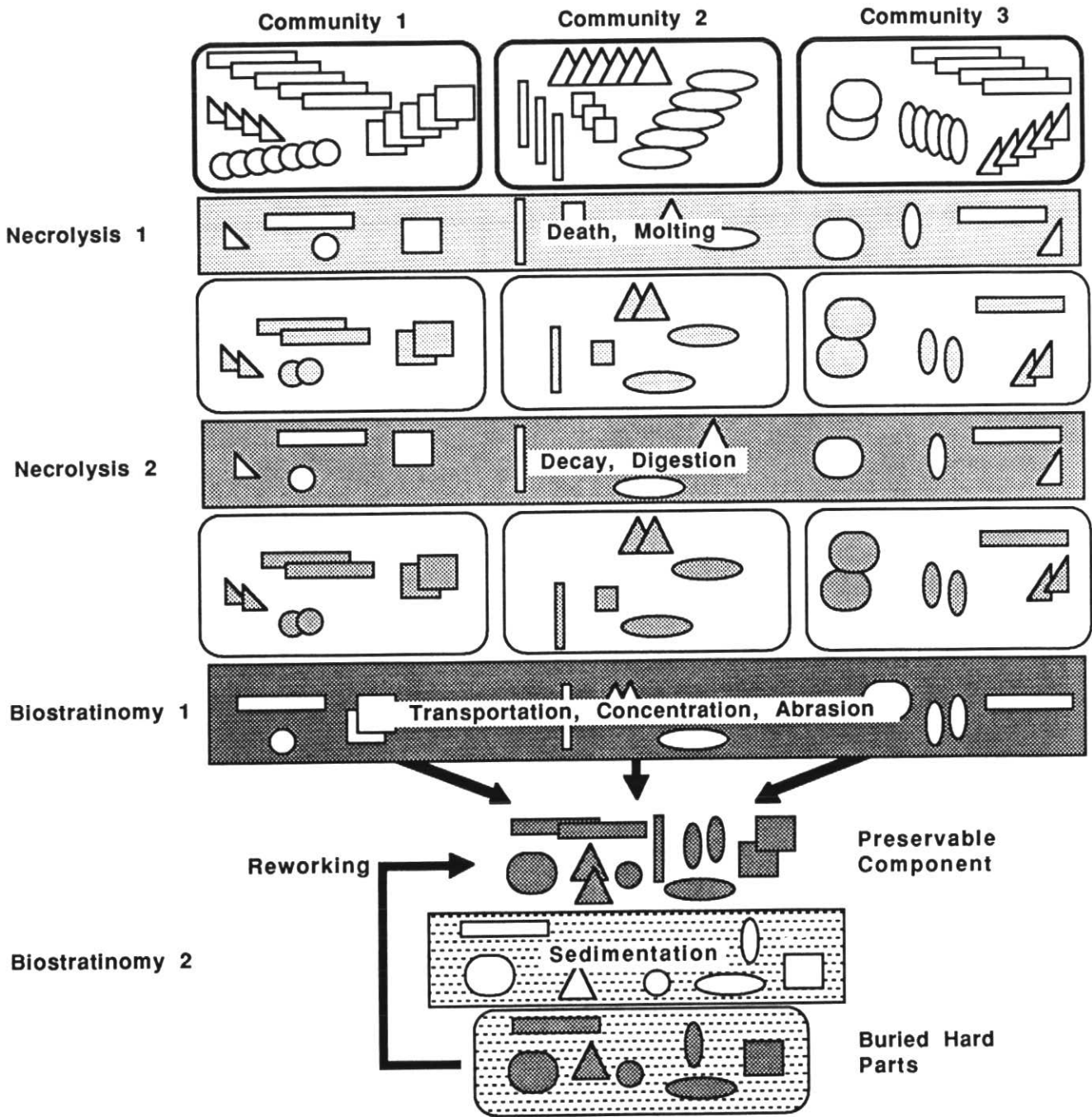
Figure 1 *Diagram of necrolytic and biostratinomic taphonomic processes illustrating some of their results: selection, mixing, and alteration. Living communities and the samples derived from them are shown as rounded boxes. Remains of animals and plants are portrayed as objects of different shapes within the rounded boxes. Necrolytic and biostratinomic processes are shown in two stages each, as shaded templates through which the remains of organisms must pass before they can be incorporated in the fossil assemblage. Selection is indicated by the reduction in numbers and kinds of hard parts caused by passage through each stage of the taphonomic process. Mixing is indicated by the combination of remains derived from different living communities. Alteration is indicated by progressively darker shading of the remains. Other processes (not shown) such as diagenesis, erosion, collection, and preparation further alter a sample of fossils before it gets to the drawer in the museum cabinet.*

methods of analysis with taphonomy. Therefore, taphonomic analysis should precede paleoecologic reconstruction, but taphonomy does not include paleoecology (Lawrence 1968, 1971).

Another possible viewpoint that is also extreme, but in the opposite sense, is that taphonomy is little more than part of paleoecology (paleoecology of predators, scavengers, bacteria, and so on), combined with part of sedimentology (fossils treated as sedimentary particles). This view contains much truth. However, a similar statement could be made about many other interdisciplinary areas of geology and biology. The real reason taphonomy exists as a separate field of study is that when left to paleontologists and sedimentologists working in isolation from each other, taphonomic experiments and analysis were seldom done and taphonomic effects were little understood.

Taphonomic Method
Taphonomists work by studying present events of death and burial, either through observation of naturally-occurring processes, through controlled experiments, or through simulations. These observations provide generalizations that can subsequently be applied to studies of fossils.

"Aktuopalaeontology", as in work on North Sea and other situations that are summarized by Schäfer (1972), is the observation of natural events for the purpose of drawing paleontological analogies. Another example is the study of modern crinoid taphonomy by Meyer and Meyer (1986). Studies that employ flumes, aquaria, or field enclosures are examples of controlled experiments. Transportation and decay of soft-bodied invertebrates was studied experimentally by Allison (1986). Field enclosures have been used to study implosion at depth of *Nautilus* (Westermann and Ward, 1980) and post-mortem destruction of shrimp (Plotnick, 1986). Death, decay, weathering, transportation, disarticulation, sorting, concentration, deposition, and reworking can all be studied through experiments. Examples of simulations are models of population dynamics and size-frequency distributions in attritional and catastrophic fossil assemblages (Craig and Oertel, 1966), and models relating fossil concentrations to sedimentation and erosion rates (Kidwell, 1986).

Once they have observed or modeled present events, taphonomists compare the living community with the buried remains, looking for characteristic patterns of difference. These differences may involve alteration or bias (selective presence or absence) of specimens or species. How the taphonomist approaches this part of the job depends on which of the two opposing trends regarding the application of taphonomy to specific problems that is emphasized.

The more traditional taphonomist sees differences as detrimental because taphonomic events produce successively more restricted subsets of the living fauna, ending with the curated sample in the museum drawer. This point of view ("taphonomic loss") has often been portrayed in diagrams (Clark et al., 1967, fig. 53; Wilson, 1988, fig. 10). A more detailed but similar diagram portrays a series of selective screens or filters that reduce information (not just diversity) available to the paleontologist (Behrensmeyer and Kidwell, 1985, fig. 3).

Elder and Smith (1984), Elder (1985), Behrensmeyer and Kidwell (1985), and Brett and Baird (1986) have recently drawn attention to the potential of an alternative approach (here termed "taphonomic gain"), in which events of fossil preservation are treated as natural experiments that shed light on physical and biological features of the ancient environment. Given certain important assumptions, one can reconstruct many of these processes, because they leave recognizable effects upon the specimens themselves, or upon the composition of the assemblage. Identifying the processes yields information about the depositional and postdepositional environment.

Figure 1 illustrates the reciprocal nature of the loss and gain approaches through an example in which necrolytic and biostratinomic processes have three main effects: selection, mixing, and alteration. Each step or process is portrayed as a template whose characteristic effects can potentially be recognized in the fossils themselves. With regard to selection, the diversity in taxa, anatomical parts, and growth-stages that was present in the original communities of living organisms is selectively restricted by each taphonomic process. With regard to mixing, taphonomic processes can actually increase taxonomic diversity above what might be present in any one community, by combining representatives of different

communities, both geographically and temporally, in one fossil assemblage. Finally, with regard to alteration, each taphonomic process can alter fossils in recognizable ways. The result in this example is a fossil assemblage that contains less information of certain kinds than was present in the source communities, yet more information of other kinds than would have been available from any one community, no matter how faithfully preserved. While not an easy task, it is possible to both compensate for some of the lost information, and recognize and extract some of the added information.

Taphonomic Loss
Much research has emphasized the causes and effects of taphonomic information loss for the reconstruction of ancient communities, for testing theories about the geometry of evolution, and for determining population characteristics of fossil species. The implications of taphonomic loss for biostratigraphy and systematics are potentially as profound but have yet to be explored as fully. Each of these research goals is considered separately below.

Reconstruction of Ancient Communities. Taphonomic processes make the reconstruction of ancient communities very difficult. Disarticulation, alteration and destruction within a community, as a result of predation, scavenging, decay, dissolution, transportation, and abrasion, cause a loss of diversity. Moreover, samples become spatially and temporally averaged. Mixing as a result of transportation causes spatial averaging, and mixing as a result of reworking is a cause of temporal averaging. Malinky and Mapes (1982), for instance, give an example of transportation effects in which terrestrial plants are preserved with marine animal fossils. Walker (1987) reviews evidence for transportation of larval exuviae (molted skins) of aquatic midges within lakes and from rivers into lakes. Wilson (1980, 1988) describes lacustrine fossil assemblages that combine freshwater fish with terrestrial plants and insects in an off-shore/on-shore gradient. Baird et al. (1985, 1986) discuss gradients of mixing between terrestrial and marine fossils in a Pennsylvanian delta.

Especially problematic are situations in which spatially averaged fossil assemblages appear to represent real communities (Gastaldo, 1987). As Figure 2 shows, it is possible that species that do not co-exist in any real

Figure 2 *Spatial mixing, as a result of transportation, can result in changes in both diversity and relative abundance of species in the fossil assemblage, as compared with the living community. In this hypothetical example, each of the two fossil assemblages consists of two common species and four rare species, but the communities from which they were derived each contains only two equally-abundant species. Only approximate geographic distributions of the species can be reconstructed from the distribution of the fossils.*
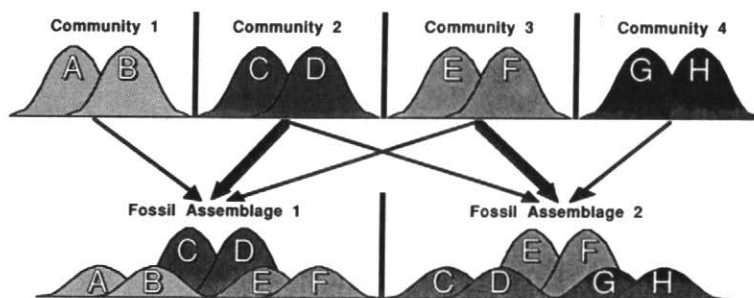
community will be preserved in the same fossil assemblage. Moreover, sampling effects alone will often cause rare species to be missed, even with large sample sizes (Badgley, 1982; Buzas et al., 1982). Only extensive sampling can sort out the major features of geographic variation in such cases, and results should never be interpreted on too fine a scale.

Spatial mixing or averaging is recognized as a blessing as well as a curse, depending on the scale of the phenomenon that is being reconstructed. Among the benefits of spatial mixing are that mixed assemblages can contain many more species than are present in any one local area, because fossils are derived from areas of non-deposition. Such mixed assemblages can be especially useful for biostratigraphic work or for faunal reconstructions that are of regional scale.

Research in the reconstruction of ancient communities has proceeded somewhat separately in each of the following taxonomic and environmental settings.

Fossil-Lagerstätten. Some examples of reconstructed communities are justifiably famous precisely because taphonomic processes have had less impact on them than on most fossil assemblages. These unusual deposits are termed "Fossil-Lagerstätten", or in English "paleontological bonanzas", and certain examples have been intensively studied (e.g., Seilacher, 1970; Seilacher et al., 1976; Seilacher et al., 1985). The Cambrian Burgess Shale of British Columbia (Conway Morris, 1985, 1986) is a well-known example in which many soft-bodied organisms are preserved, reinforcing the lesson that only a fraction of the diversity is normally preserved in the fossil record, but many other examples are known around the world, such as Ediacara (late Precambrian), Holzmaden (Early Jurassic), and Solnhofen (Late Jurassic). One family of Fossil Lagerstätten involves preservation of soft parts or three-dimensional remains in various kinds of nodules (Müller, 1985; Baird et al., 1985, 1986; Phillips and DiMichele, 1981; Scott and Rex, 1985). Some other examples of unusual fossil concentrations are summarized by Gall (1983) and by Whittington and Conway Morris (1985). In some unusual situations, catastrophic or sudden death captured temporally-restricted "snapshots" of ancient communities, for example by rapid burial. A possible example of this type is shown in Figure 3. In other cases, special physical and biological conditions such as anoxia and lack of physical and biological disturbance led to excellent preservation of specimens over long periods of time.

The study of Fossil-Lagerstätten has also recently been linked to the concept of "event stratigraphy" (Einsele and Seilacher, 1982; Aigner, 1985), which is the search for and interpretation of unique events in earth history through recognition of their signatures in the sedimentary record. On a large scale, these could be volcanic eruptions or landslides. On a small scale, they could be storm deposits, condensed beds, or layers of mud cracks. Sedimentological signatures of physical events are particularly valuable for reconstructing the environment of older fossil deposits because the alternate strategy of uniformitarian extrapolation of biological processes becomes much less reliable over longer spans of geologic time. Conversely, fossil concentrations and taphonomic characteristics can be useful for identifying event beds.

Marine Invertebrate Communities. Most recent authors agree that taphonomic loss is severe in marine habitats. For example, in a
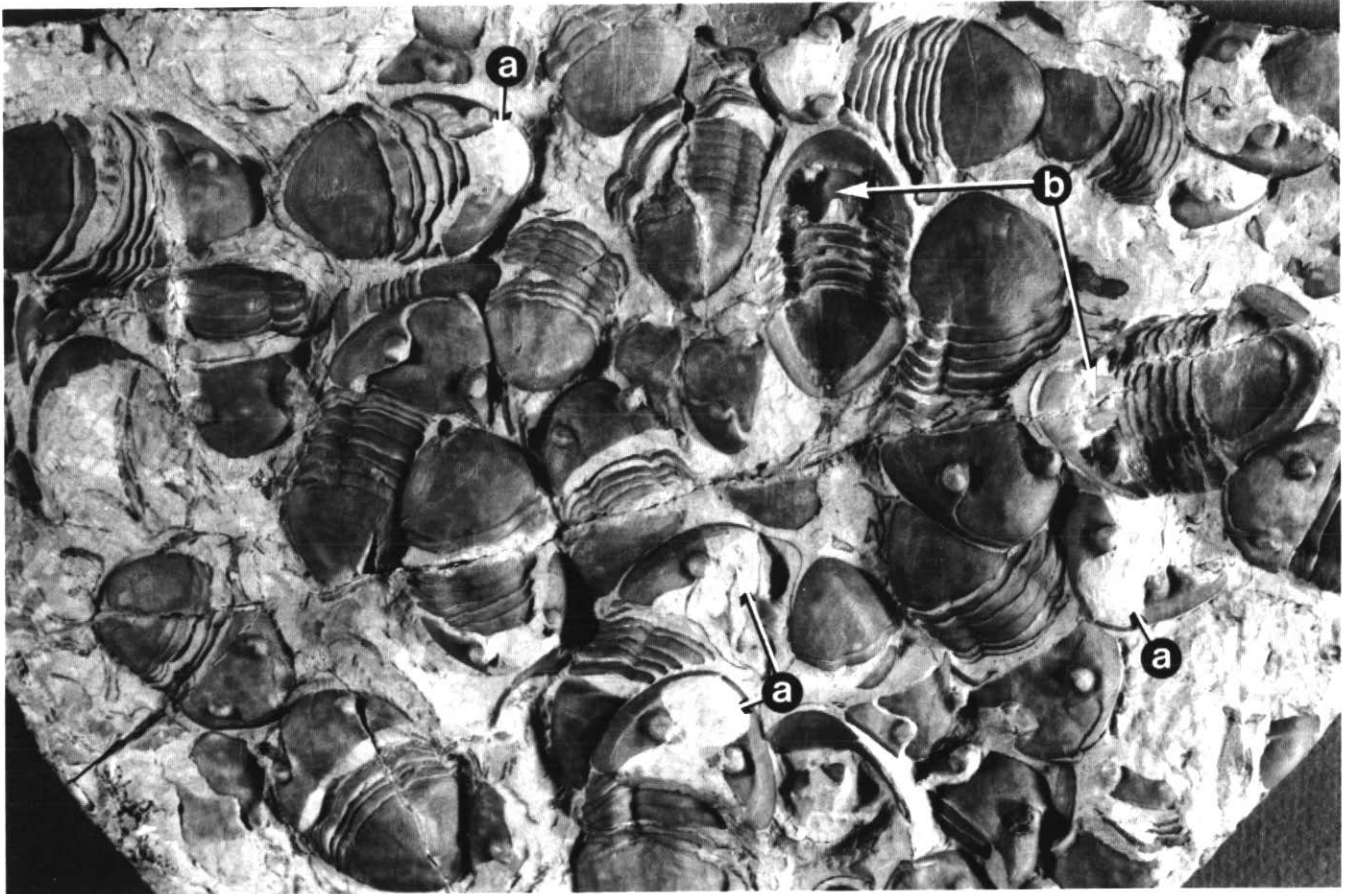
Figure 3 *Part of a trilobite "Lagerstätten" from the Middle Ordovician Bromide Formation of Oklahoma, USA. The trilobites* (Homotelus bromidensis) *represent mostly intact, upright, dead individuals but also include some possible molted exoskeletons and some upside-down dead individuals. Aggregations of articulated specimens such as these can be caused by rapid, deep burial in sediment, by chemical poisoning, or by suffocation. Although rapid burial may not have been a cause of death, burial must have followed quickly because the trilobites remain fully and tightly articulated.* **(a)** *probable molted exoskeletons are distinguished by absence of the central glabellar portion of the cephalon.* **(b)** *intact, upside-down, dead individuals showing hypostome still in articulated position.*

study of the potential for fossilization of a modern intertidal fauna based on habitat, hard parts, and known fossil record, Schopf (1978) estimated that only about 40% of the macroscopic fauna is preservable in the fossil record.

Taphonomic loss in marine invertebrate communities is seen as due to destruction and local reworking, more than to transportation. A fossil assemblage derived from one of these habitats is likely to contain species from the same geographic location, although not necessarily the same time, and many members of the original community will be missing through selective destruction.

Researchers have pointed out that destruction by scavengers, predators, decay, abrasion, and dissolution is selective in these communities. Even for shelled organisms, destruction is selective by size: half of the smallest mollusc shells are destroyed within 100 days of death (Powell et al., 1984; Cummins et al., 1986). It is not only organisms with calcareous shells that are rapidly destroyed. Rapid destruction of shrimp carcasses by scavengers and bacterial decomposition was reported by Plotnick (1986) using both field and laboratory experiments. Moreover, infaunal organisms are more likely than epifaunal ones to die within the sediment where their hard parts can be preserved. Kier (1977) pointed to the correlation between the infaunal habits of irregular echinoids as compared with epifaunal regular echinoids and the much more diverse fossil record of the former. Selective destruction also means that trophic relationships are difficult to reconstruct because they can be badly distorted, for example through loss of soft-bodied organisms (Stanton, 1976) and calcareous skeletons. As a practical application, Peterson (1976) advocated using simple occurrences of species in paleoecology, rather than their relative abundances, because the former are less likely to be altered by taphonomic biases.

In contrast with in situ destruction, sorting and spatial mixing as a result of transportation cause relatively little loss in marine invertebrate communities. Hoffman (1979), Peterson (1976), Stanton (1976), Warme (1969), and Warme et al. (1976) all agree that spatial distributions are usually little altered by transportation after death in many modern near-shore marine habitats. A possible exception is the effect of diving birds (see above). Also, opinions differ on the extent of post-mortem transportation reflected in the Burgess Shale assemblage (Allison, 1986).

Terrestrial Vertebrate Communities. Early workers in paleoecology of terrestrial vertebrates tried to reconstruct ancient communities from fossils and sedimentological evidence (e.g., Shotwell, 1955; Voorhies, 1969; Dodson, 1971), but without the benefit of much knowledge of taphonomic processes in modern communities. Despite this limitation, they recognized the fundamental importance of transportation and its effects, including faunal mixing and progressive disarticulation and destruction of skeletons.

More recently, some authors have examined taphonomic loss in modern assemblages, concentrating on African mammals. In a simulation study, Badgley (1982) used life-history features of modern African mammals to make computerized models of temporally-averaged fossil assemblages. She found that fossil samples would only accurately reflect true relative abundances of species if large sample sizes (> 1000 specimens) were obtained. Behrensmeyer (1975, 1978), Behrensmeyer and Hill (1980), Behrensmeyer et al. (1979), and Hill and Behrensmeyer (1984) have compared modern African mammalian communities with assemblages of dead and decomposing carcasses, and also with geologically young fossil assemblages preserved in fluvial sediments. One of their conclusions is that relative abundances of species in the fossil assemblage are not usually an accurate reflection of relative abundances in the community (Behrensmeyer et al., 1979; this conclusion is similar to that reached by students of marine invertebrates). A second conclusion is that spatial distribution of large-mammal carcasses on the surface of the ground accurately reflects distribution of living animals, except for migratory species (Behrensmeyer et al., 1979). This may mean that causes of death and subsequent destruction in situ are not very selective overall. Many of these carcasses must be subject to fluvial transportation before they reach their ultimate destination, so that fossil assemblages might still be biased by transportation. A third important conclusion is that species with small body size are systematically under-represented in assemblages of carcasses on the surface of the ground (Behrensmeyer et al., 1979) as compared with living communities. A similar conclusion was reached by Damuth (1982), who compared sizes of bones in modern communities against sizes in assemblages of fossil vertebrates.

Terrestrial Plant Communities. Like vertebrate paleontologists, paleobotanists have also recognized the importance of transportation as a source of taphonomic loss. As with terrestrial vertebrates, terrestrial plants are almost always preserved some distance from where they lived and under aquatic rather than terrestrial conditions. As a result, the likelihood that fossil "floras" are potentially very biased by sorting and mixing has been fairly widely appreciated (e.g., Krasilov, 1975; Gastaldo, 1987), particularly among palynologists who daily face evidence of reworking, contamination, and potential long-distance transport (Gray, 1985). However, without evidence from modern habitats, or broad comparative analyses of fossil assemblages, the precise nature of the biases was not understood. Recent studies have contributed in both of these areas.

Studies based on modern habitats include observations on capture, transport and deposition of plant remains by rivers (Holyoak, 1984; Scheihing and Pfefferkorn, 1984; Teslenko, 1980), and on distribution of taxa, sizes, and shapes of leaves in deltaic and lacustrine environments (Roth and Dilcher, 1978; Spicer, 1980, 1981). Stream-side plants are predictably over-represented in many fluvial assemblages. The composition of lacustrine and deltaic assemblages depends on the resistance of different plants to mechanical and biological destruction, as well as on their susceptibility to transport by wind and water. Small "sun leaves" (usually found on the upper branches) of deciduous forest trees are proportionately more common in open-lake deposits than in river sediments or near-shore deposits. Larger "shade leaves" are actually more easily carried by wind because of their greater ratio of surface area to volume, but are apparently not normally exposed to sufficiently high wind velocities and end up being more common in near-shore sediments.

Comparative analyses of fossil assemblages include studies of Eocene and Miocene lacustrine deposits. Studies on co-occurring plants, insects, and fish in Eocene deposits led to conclusions similar to those based on modern habitats: deciduous leaves (and wood fragments) are proportionately more common in open-lake sediments (Wilson, 1980, 1988), whereas conifer leaves, including needles, are proportionately more common in near-shore sediments. Gray (1985) analyzed co-occurring assemblages of plant megafossils and pollen in a Miocene stratigraphic section. Among her conclusions are that plant microfossils represent many groups for which no megafossils are found, while megafossils provide greater taxonomic resolution. Megafossil abundances are more variable than pollen abundances, apparently because of sedimentological effects.

In summary, fossil assemblages of terrestrial plants have been subjected to severe taphonomic loss due primarily to transportation. Spatial distributions, relative abundances of species, and relative proportions of different plant organs are all biased as a result. Therefore, paleobotanists must not base interpretations of paleoclimate on a single assemblage unless the taphonomic influences on its composition are relatively well understood. Moreover, they should be aware that artifactual plant successions can result, as Krasilov (1975) pointed out, from changes in taphonomic conditions (for example through transgression or regression in a lake; Wilson, 1980, 1988).

Geometry of Evolution. Taphonomic loss must also be appreciated by those currently debating the geometry or mode of evolution and the related question of the paleontological species concept. If the "punctuated equilibrium" hypothesis of the geometry of

Figure 4 *An example of temporal averaging caused by tiering. These two hypothetical bivalves (drawn to resemble the modern razor clam* Siliqua patula, *a species capable of burrowing to considerable depths) died in the same layer of sediment, yet the one on the right could be geologically much older than the one on the left. The specimen on the right died on the surface of the sediment, where its elastic ligament caused its shell to open. It was then buried under more sediment. The specimen on the left then burrowed vertically into the sediment, where it died. The two specimens could thus have lived thousands of years apart.*
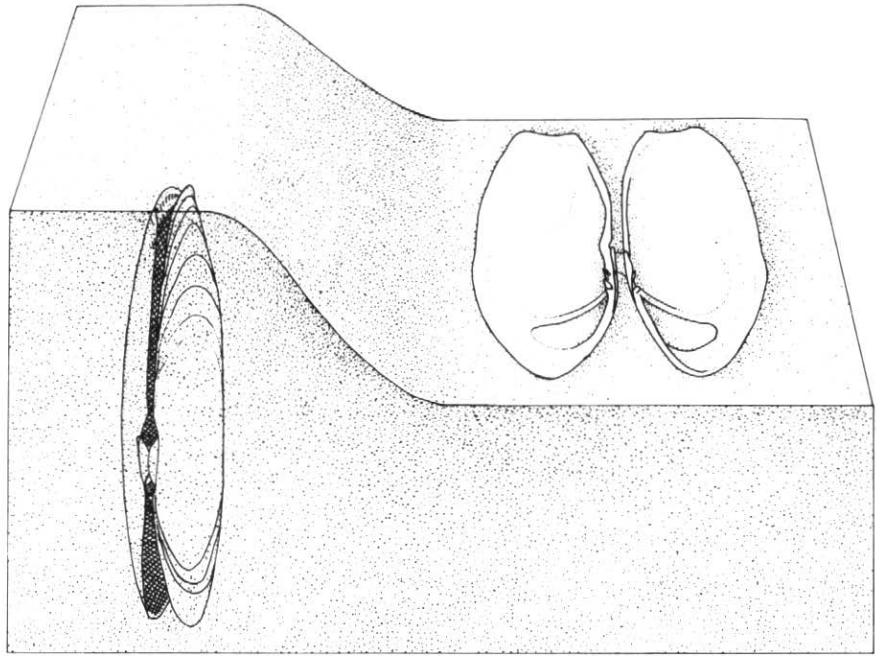
Figure 5 *Recognition of reworked specimens. (A) A shell that has not been reworked has a sedimentary filling that matches the sediment that surrounds the shell. In addition, crystals of sparry calcite fill the upper part of the shell, and the contact between sediment and crystal fillings is parallel to bedding. The result is an indicator of the original orientation of the shell, an example of a "geopetal" structure. (B) A reworked shell can contain a sedimentary filling that does not match the sediment that surrounds it. In addition, the boundary between the sedimentary filling and the crystalline filling is not necessarily parallel to the bedding planes. In addition to the characteristics illustrated, reworked specimens can also differ in colour or have different kinds of crystalline fillings from unreworked specimens in the same layer, because of their different chemical history, and can show greater effects of abrasion due to weathering and transportation. (After Gall, 1983).*
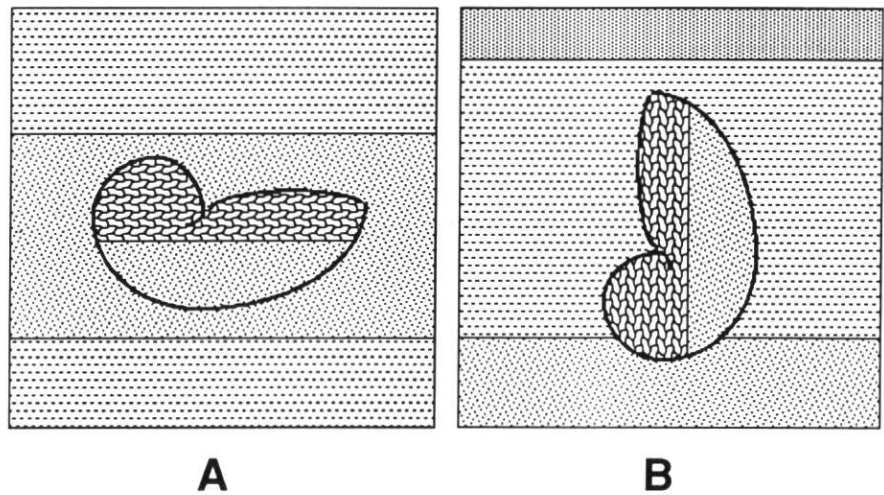
Figure 6 *Diagram to illustrate the relationship between rate of fossil (hard-part) input and rate of sedimentation in the origin of concentrations of fossils. Units are arbitrary. Fossil concentration is the ratio of fossil input to sediment input. When sediment input is zero but fossil input continues (thick vertical lines), high concentrations of fossils can result (arrows). Erosion of sediment can produce even greater concentrations of fossils in the form of lag deposits.*
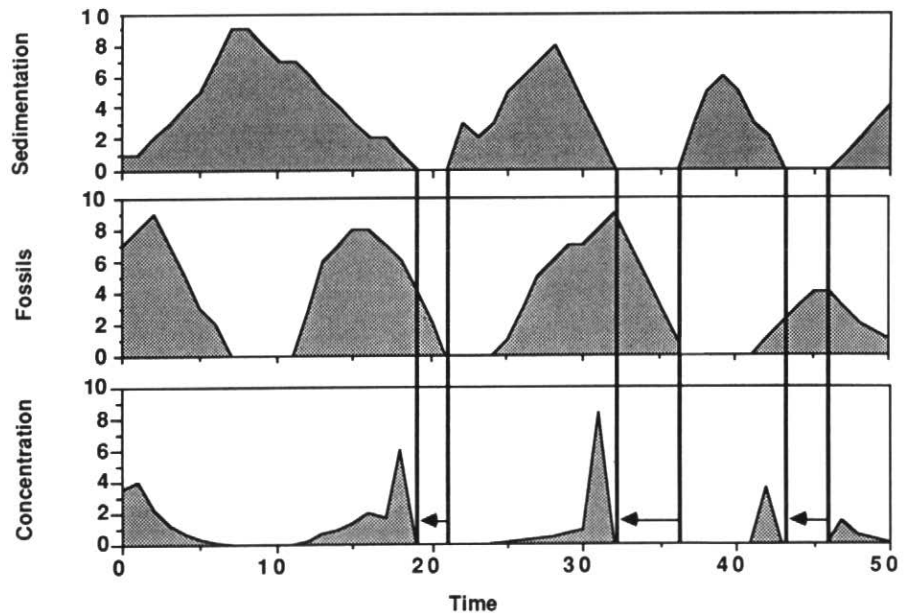
evolution (Eldredge and Gould, 1972) is correct, species are naturally distinct. In other words, if species arise abruptly ("punctuation") and then remain relatively unchanged ("stasis"), it will be easy to distinguish them from their ancestors and descendants because they will be separated by distinct morphological gaps. On the other hand, if the "gradualism" hypothesis is correct and species originate and change by accumulation of small incremental changes, there are no distinct gaps between ancestors and descendants, and the divisions between them are arbitrary (Fox, 1986). On the one hand, the geometry of evolution is said to be rectangular, and on the other hand it is said to be curvilinear.

What the taphonomic perspective can contribute to this debate is that tests of these hypotheses are influenced by taphonomic loss, especially by temporal mixing. The variability of morphological features in samples of fossils can be much affected by sampling strategy and by taphonomic effects such as reworking. Specifically, the "stratophenetic" test is vulnerable.

"Stratophenetics" was originally introduced by Gingerich (1979) as a method of reconstructing phylogeny by linking structurally similar samples of fossils, over time, in highly-resolved stratigraphic sequences. The method has also been advanced as a test of the "punctuated-equilibrium" hypothesis (Gingerich, 1982). In the stratophenetic test, one tries to measure morphological variability within and between samples in order to determine rates of evolution and to distinguish between examples of stasis plus punctuation and examples of gradualism. The vulnerability of this test lies in the fact that measurements of rates of evolutionary change can be underestimated or overestimated, as a result of temporal averaging.

Causes of Temporal Averaging. Some causes of temporal averaging, for example difficulty in tracing contemporaneous bedding planes and coarse sampling procedures, are not, strictly speaking, a matter for taphonomic investigation. The causes of temporal averaging that are a direct result of taphonomic processes are the causes of temporal mixing: tiering, reworking, and lag deposits.

Tiering is the layering of burrowing organisms at different depths within the sediment (Bottjer and Ausich, 1982). Tiered organisms can die and be preserved at considerable vertical distances from the sediment-water interface. This means that specimens of these species in any layer of sediment could actually represent organisms that lived thousands of years after the sediment was deposited (Figure 4).

Reworking causes the opposite effect to tiering. In reworking, fossils are eroded or bioturbated from older sediment and then redeposited: reworked fossils represent organisms that lived prior to the time of final deposition (Figure 5).

Lag deposits resemble reworked deposits. As concentrations of fossils formed without accompanying deposition of sediment or remaining after erosion of sediment, they actually represent more time than the sediment itself (Behrensmeyer and Kidwell, 1985). Lag deposits may be very common, especially for organisms with hard parts that are resistant to dissolution and abrasion, such as phosphatic conodont elements and vertebrate bones and teeth. Estimates of the temporal interval represented by lagged bone beds in marine shelf environments range up to a million years (Norris, 1986). In one study, bone beds were found to be concentrated near the middle of the continental shelf, at or just below storm wave base (Norris, 1986). However, lag deposits are often unrecognized. Instead it is often assumed that these fossil concentrations represent periods of time with high fossil input such as periods of high death rate. Kidwell's (1986) "R-sediment model", developed through simulations and comparisons with actual fossil concentrations, illustrates the effect of lag deposits (Figure 6). Its applicability may be somewhat limited in the case of remains that are subject to dissolution and abrasion, such as calcareous shells, which other studies discussed above (*e.g.*, Powell *et al.*, 1984) show have a short half life in marine environments.

Fossil soils (Retallack, 1984) represent the special case of subaerial lag deposits. Examples of fossils from fossil soils are the specimens used in the original application of stratophenetics: Gingerich's (1979) mammalian fossils, collected from the Willwood Formation (each sample representing about 27,000 years according to Gingerich, 1982). The vast majority of geologic time can be missing from such sections: Sadler (1981) and Sadler and Dingus (1982) estimate fluvial formations such as the Willwood to be about 100 times less complete than certain deep-sea drill cores.

Effects of Temporal Averaging on Measured Rate of Evolution. The problem with using stratophenetics to distinguish between lineages that exhibit stasis plus punctuations and those that are evolving gradually is that lineages can appear to exhibit either false stasis or punctuation or false gradualism, as a result of temporal averaging. False stasis can be caused by temporal averaging of samples from a lineage that is changing more rapidly than is detectable by the density of samples available, but in which the direction of change reverses often (see for example Bell and Haglund, 1982). Samples from such a lineage should have greater variability than samples from an otherwise equivalent lineage with true stasis (Bell and Sadagursky, 1986), but with little or no long-term change in average morphology. In fact, the variability of any morphological feature in a sample of fossils is proportional to both rate of evolution and the amount of time that the

sample represents (Figure 7). Evolutionary rates can also be under- or over-estimated when instantaneous sedimentation rates are high but the stratigraphic section is very incomplete: a lineage will appear to change very little over a thick segment of section (but this is actually because so little time is represented in this segment), then change abruptly at the sedimentary discontinuity, which represents a large amount of time. On the other hand, false gradualism can result if samples are temporally averaged over spans of time longer than the periods of true stasis and punctuation. Therefore, it is not surprising that both "punctuationalists" and "gradualists" have accused each other of failing to resolve the true geometry of evolutionary change in their tests.

Therefore, temporal averaging can interfere greatly with measurement of rates of evolution. Incomplete or temporally-mixed sections may be adequate for measuring net long-term rates of evolution because short-term evolutionary changes are averaged out, particularly if the sections in question span a great deal of time and if they are capable of yielding large sample sizes. For accurate measurement of short-term rates of change, one must choose study sections in a way that maximizes completeness and minimizes temporal averaging. Varves (annual layers), usually deposited in lacustrine environments, are an example of a situation that comes close to meeting these criteria (Bell and Haglund, 1982; Wilson, 1987). However, such sections often represent a short total span of time and lack large samples of fossils.

Population Characteristics of Fossil Assemblages. Much of traditional paleobiology and paleoecology has been concerned with reconstructing aspects of the life history of fossil species. Although most fossil samples are temporally averaged to some extent, whether it be over months, or over thousands of years, and although many population processes fluctuate on a much finer time scale than can be resolved in the fossil record (Peterson, 1976), some life-history information can be reconstructed. Examples of items of interest are numerical abundance, habitat and trophic proportions, biomass, growth rate, mortality and survivorship.

Staff *et al.* (1986) argue that numerical abundance and trophic and habitat proportions are difficult to estimate in fossil assemblages, whereas estimates of biomass are less susceptible to taphonomic loss because they are not as variable over short time intervals.

Growth rates, mortality, and survivorship can be reconstructed from age-frequency distributions, which can sometimes be reconstructed from size-frequency distributions. However, some recent work suggests that taphonomic rather than population processes control the size-frequency distributions of marine molluscs (Cummins *et al.*,
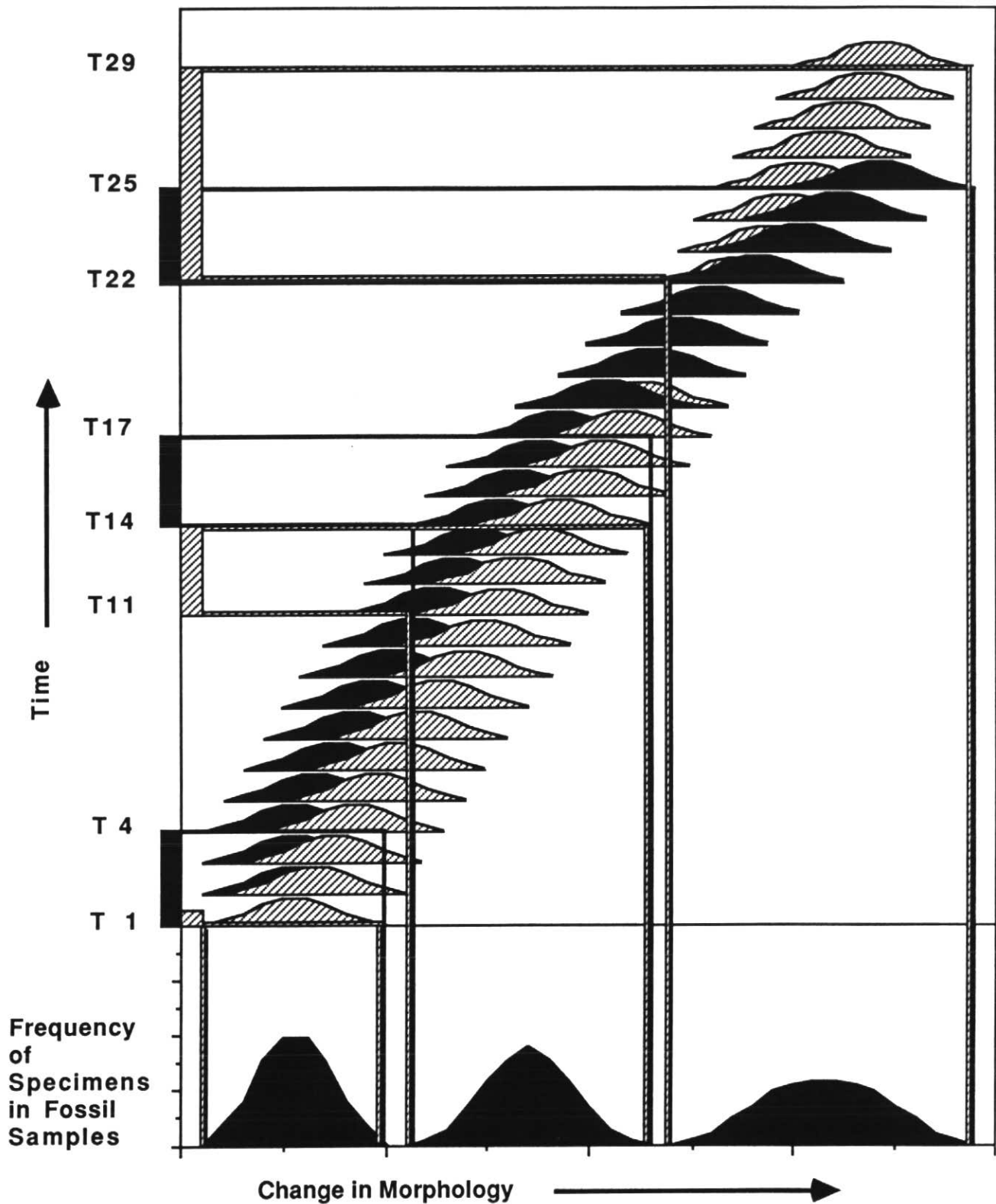
Figure 7 *Morphological variability of a fossil sample varies directly with both rate of evolution in the species and temporal duration of the sample. This is illustrated by two evolving lineages represented by small "bell" curves in the upper part of the diagram, and three temporally averaged samples, represented by the three large "bell" curves in the lower part of the diagram. The thick black and cross-hatched bars along the vertical time axis represent the intervals of time spanned by the fossil samples.*

The lineage represented by hatched curves evolves at a constant rate throughout the section. The lineage represented by black curves remains unchanged for the first four units of time, then evolves at the same rate as the other lineage, and finally evolves at twice the rate of the other lineage. The left-hand sample from the hatched lineage, representing a single time unit (T1), has the same amount of variability as a sample from the black lineage representing four time units (T1-T4), because the black lineage does not change over this interval. The middle samples are drawn from lineages evolving at equal rates, and the temporal durations of the samples are also equal (four time units), resulting in equally variable samples (but more variable than those to the left). The right-hand samples represent different temporal intervals and are drawn from lineages evolving at different rates, but the samples are equally variable because the two effects exactly cancel each other in this case. The sample from the black lineage represents four time units (T22-25) while the sample from the hatched lineage represents eight time units (T22-29). The rates of evolution also differ by a factor of two, but in this case the black lineage has the greater rate, the hatched lineage the lesser rate. The right-hand samples are more variable than those to the left because of the greater temporal interval (hatched lineage) or the greater rate of evolution (black lineage).

1986), particularly by removing small specimens. Rapid selective loss of small shells (Powell et al., 1984) has not uniformly been observed. For example, Noble and Logan (1981) found that neither predation nor fragmentation by turbulence significantly affected the size-frequency distribution of brachiopods in a modern high-energy environment.

Just because fossils have a certain size-frequency distribution, it cannot be assumed that the living population had a similar distribution. There are two common criteria for deciding whether a given distribution is unbiased by taphonomic processes. One criterion is a comparison of actual size-frequency distributions against theoretical or modern ones, on the assumption that distributions that are most like the theoretical ones are the least altered (Boucot, 1953; Olson, 1957; Rigby, 1958; Johnson, 1960; Craig and Oertel, 1966; Hallam, 1972). The danger in this approach is that reconstructed life-history traits may be biased toward the theoretical expectations. The second criterion is the absence of temporal averaging, especially if provided by independent lines of evidence. Mass-death layers are usually more valuable for reconstructing the size-frequency distribution of the living population than are attritional-death layers, which are temporally mixed, although multiple mass-death layers are needed to yield information about temporal variability of size-frequency distributions.

Once the size-frequency distribution has been reconstructed, it can be transformed into an age-frequency distribution if the age at death of some of the specimens can be

determined. Age can often be inferred from annuli on skeletal elements, especially in organisms with indeterminate growth. Organisms with both seasonal growth and synchronous seasonal reproduction can also exhibit year-class peaks in the size-frequency distribution of the living population, which are helpful in reconstructing the relationship between size and age at death (Craig and Oertel, 1966; Wilson, 1977b, 1984). Again, mass-death layers are more likely to provide this information. However, a temporally-averaged sample of Eocene freshwater fish also shows year-class peaks in the size-frequency distribution, because the fish died annually during the non-growing season (Wilson, 1984).

Biostratigraphy. Taphonomic loss is also a concern to biostratigraphers, because taphonomic processes can control both first and last appearances of index fossils in the rock record. The four possibilities are false late appearance, false early extinction, false late extinction, and false early appearance.

As it is very unlikely that the very first members or the very last members of a species will be preserved in the rocks, false late appearance and false early extinction are common problems (Figure 8). In these cases, the fossils' geologic range is shorter than the species' true range.

It is also possible for the fossils' geologic range to be greater than the species' true range, through both false late extinction and false early appearance. False late extinction is the more likely and often more severe of these two problems. It can be caused by reworking (Figure 5), by delayed deposition, and by formation of lag deposits (Figure 6).

False early origin should be much more rare and usually involve shorter spans of time. It will occur, for example, with infaunal or burrowing organisms (see Figure 4 and discussion of tiering above), and through unrecognized fissure fillings and channel deposits. One reason for giving first appearances greater weight than last appearances in biostratigraphy is that large errors due to reworking are probably much more common than large errors due to burrowing.

The debate about catastrophic versus gradual extinction of the dinosaurs illustrates these problems. Articulated dinosaur skeletons become progressively less common in Late Cretaceous rocks, and have never been found in the very latest Cretacous rocks, leading some to suggest that their extinction was gradual (Sloan et al., 1986; Sloan and Rigby, 1986). Catastrophists argue that dinosaurs survived to the very end of the Cretaceous but that their last survivors were not preserved (false early extinction). A further possibility, not usually considered because of the absence of a plausible cause, is that dinosaurs became extinct earlier, catastrophically or otherwise, and that the specimens in latest Cretaceous rocks are reworked (false late extinction). Finally, Sloan et al. (1986) have gone farther and argued that dinosaur teeth found in Paleocene sediments represent dinosaurs that lived after the Cretaceous. Others maintain that these specimens represent reworked Cretaceous dinosaur fossils (Bryant et al., 1986; false late extinction).

Systematics. Taphonomic loss causes several problems for the systematist. Disarticulation, alteration and destruction
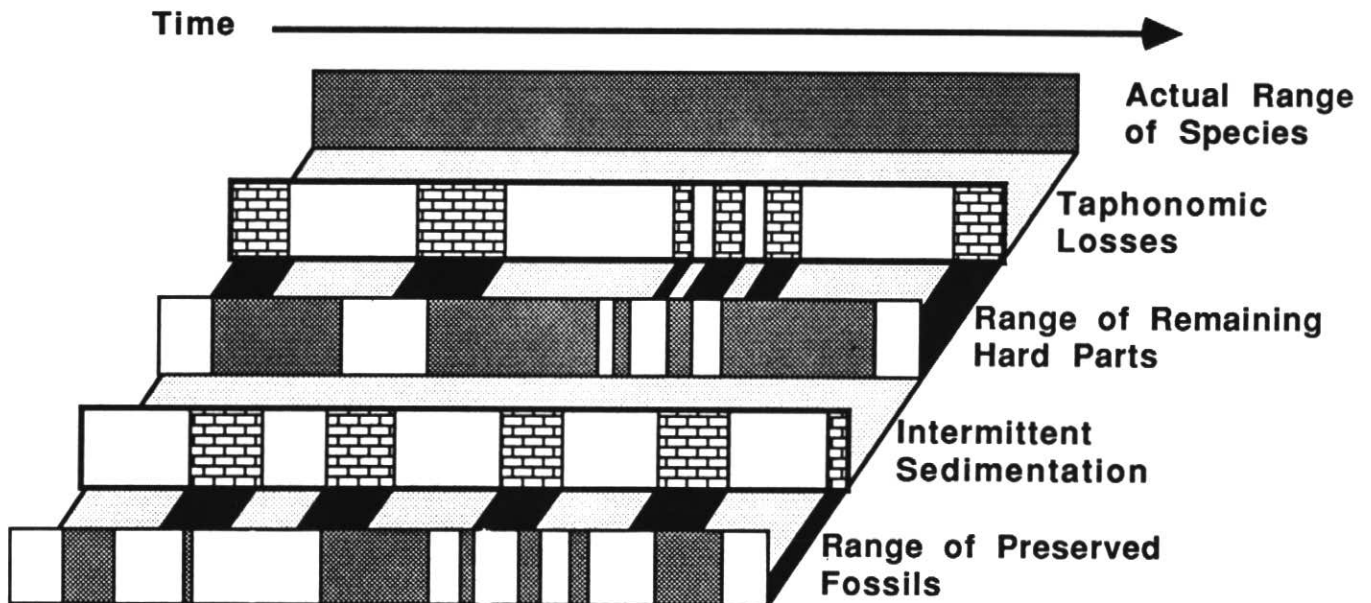
Figure 8 Diagram illustrating the most common effects of taphonomic loss (shown as wall-like barriers) on the geologic range of a fossil species (shown as shaded bars). In this example, taphonomic losses such as necrolytic biases, abrasion, and dissolution prevent remains of the species from reaching the site of potential fossilization. As a result, hard parts are not available for temporal intervals when taphonomic losses are most severe. Similarly, sedimentation is necessary for most forms of fossilization, but sedimentation is usually intermittent. As a result, the final range of the fossils in the rocks is the total range of the species, less both the temporal intervals of severe taphonomic losses, and the temporal intervals of no sedimentation.

especially make it difficult to associate parts of the same organism or species (Figure 9). Fully articulated trilobites (Figure 3) are relatively rare. Most trilobite fossils represent fragments disarticulated by decay, turbulence, and scavengers. Many other trilobite fossils represent partial skeletons that result from molting (Figure 3). Similarly, fish bones are often disarticulated and digestion by predators can alter their apparent morphology (Wilson, 1987). Crinoids are seldom found articulated but are extremely common as disarticulated remains (Figure 9; Moore and Jeffords, 1968). Lutz (1984) gives an example in which taphonomic disarticulation of cockroach wings led to erroneous creation of a new family for the resulting wing fragments; experiments with modern cockroach wings illustrated the process of disarticulation.

Even when disarticulation is recognized, as for example with conodonts, echinoderms, trilobites, and vertebrates, the paleontologist faces the problem of associating separated parts. Paleobotany provides some of the best examples of these difficulties, since separate names have been created for seedlings, roots, stems,

leaves, flowers, pollen, and seeds of one biological species (they also commonly have different apparent geologic ranges). Moore and Jeffords (1968) similarly advocated increased study of crinoid columnal segments and proposed a nomenclature suitable for the disarticulated elements. The problem can sometimes be avoided if there has been little transportation. An example of minimal taphonomic loss in paleobotany is Crane and Stockey's (1985) study of a Paleocene plant, in which seedlings and many different organs of the adult plant are known and can be assigned to a single paleontological species.

Even if fossils are perfectly preserved, temporal and spatial mixing affect the systematic work done by all paleontologists through their effect on morphological variability. Temporal mixing of a species that is changing, whether by evolution (Figure 7) or by phenotypic response to different environments, can result in greater variability in the temporally averaged fossil sample than was present in the original species at any one time. Spatial mixing of species that vary geographically can similarly result in greater variability in the sample, because the fossil

assemblage includes specimens from different regions (Figure 2), such as different parts of a river system, or different altitudes or depths. When fossil samples have unequal or larger-than-normal variance, the differences between species might not be recognized.

Taphonomic Gain

In the taphonomic-loss approach, the usual aim is to reconstruct the original condition of the fossilized species or community, in spite of the often fragmentary or inadequate condition of the fossil specimens. In the taphonomic-gain approach, the usual aim is to reconstruct the agents of taphonomic loss, thereby adding to knowledge of the ancient physical and biological environment.

A comparison with sedimentology will help to illustrate the difference: the taphonomic-loss approach is comparable to using sedimentology to reconstruct the rocks and mountains from which the sedimentary particles were derived; the taphonomic-gain approach is comparable to using sedimentology to reconstruct the weathering, transportation, or depositional environment of the sediments. It is interesting that the loss

Figure 9 *This slab of calcareous shells from the Lower Silurian Jupiter Formation of Anticosti Island records at least two different taphonomic régimes. An initial pavement of fragmented and disarticulated brachiopod valves, crinoid and trilobite fragments represents a fairly high-energy environment, possibly representing a winnowed storm lag formed below normal wave base but above storm wave base. The brachiopod valves are mostly preserved convex-side up, the typically most stable orientation under turbulence or currents. A few brachiopods in the layer beneath, not evident in this picture, are preserved articulated and contain sediment plus crystalline fillings that confirm the orientation of the sample (as in Figure 5A). Subsequent to the formation of the storm lag and under conditions of diminished current, specimens of (possibly benthic) ostracods came to lie between and on the shells. (a) specimens of the ostracod species Zygobolba anticostiensis. (b) valves of the orthid brachiopod Coolinea alterniradiata. (c) free cheek of the trilobite Encrinurus deomenos.*

approach has predominated in taphonomy until recently, whereas the gain approach has predominated in sedimentology.

The difference between the loss and gain approaches is illustrated in the case of predation, which can be a selective cause of death, a mechanism of transportation, a cause of breakage, disarticulation and dissolution, and an agent of concentration and deposition. The loss-oriented taphonomist is satisfied to recognize the effects of predation on a fossil assemblage. Once he understands to what degree the assemblage has been altered, he can proceed with his main task of reconstructing the aspects of the fossilized species in which he is interested, such as its articulated skeleton and its life habitat. The gain-oriented taphonomist, on the other hand, is more interested in the predator. He wishes to understand as much as possible about the identity of the predator, and what the presence and activities of the predator tell us about the ancient environment.

Taphonomic gain has resulted from the work of several taphonomists who have reconstructed predation in both terrestrial and aquatic situations. They have proposed criteria for distinguishing preyed-upon remains from other remains, and for identifying which predators were involved. Andrews and Evans (1983) studied the effects of bird predation on bones of small mammals in the Recent. Haynes (1980, 1983) learned to recognize damage done to bones of large mammals by mammalian carnivores. Examination of fossilized gastric pellets and/or fecal material, containing bones of small vertebrates, has demonstrated the activity of owl, hawk, and mammalian carnivore predators in the fossil record (Dodson and Wexlar, 1979; Fisher, 1981; Mayhew, 1977). In shallow marine sediments, anomalous occurrences of shells of deep-water molluscs is evidence for the activities of diving birds (Lindberg and Kellog, 1982). In freshwater sediments, gastric pellets containing concentrations of disarticulated, partly-dissolved fish bones point to piscivorous aquatic birds, even in formations where bird fossils themselves have yet to be found (Wilson, 1987).

Other aspects of the environment pertaining to the interval between death and burial have been reconstructed also. Behrensmeyer (1978) and Hill and Behrensmeyer (1984) helped portray the site of death of large African mammals by studying the effects of exposure on Recent bones. Also, water depth and sedimentary history have been reconstructed from studies of cephalopod shells. Shells that are imploded or imbedded vertically in soft sediments were cited as evidence of different water depths, based on experiments with Recent specimens of Nautilus (Weaver and Chamberlain, 1976; Kanie et al., 1980; Westermann, 1985; Westermann and Ward, 1980; Hewitt and

Westerman, 1985). Aspects of the sedimentary history of the Jurassic in Germany have been deduced from how ammonites were compressed in the sediment when fossilized (Seilacher et al., 1976). Elder (1985) used taphonomic characteristics of fish skeletons to reconstruct temperature, depth, oxygen content, currents, scavengers, decay, and sedimentation rate in lacustrine environments (Figure 10). She reinterpreted the paleoenvironments of several deposits of fossil fish, including those studied by Waldman (1971), McGrew (1975), Wilson (1977a), and Zangerl and Richardson (1963).

Event beds such as storm deposits are a particularly valuable source of data (Speyer and Brett, 1988). Water depth relative to storm wave base can often be reconstructed from taphonomic characteristics of a deposit, including the size range and amount of breakage and rounding of skeletal fragments (Figure 9). Currents and/or waves can also orient skeletal remains (Müller, 1979). Orientation relative to the vertical is seen in bowl-shaped brachiopod and clam valves, which usually come to rest with the convex surface upward (Figure 9). Orientation in the horizontal plane is seen with elongate skeletal remains (Figure 11), which are often oriented parallel to paleocurrent directions and can leave drag marks in the sediment, or can be oriented at right angles to wave directions. Alexander (1986), in a two-stage application of the principle of taphonomic gain, deduced paleocurrent velocities from brachiopod orientations, which in turn were deduced from frequencies of different kinds of post-depositional deformation of the brachiopod shells.

The assumptions of taphonomic loss and taphonomic gain

The difference between the loss and gain approaches is subtle, and many researchers combine the two in their studies of individual deposits. The building blocks of taphonomic argument are similar in both: (1) aspects of the living community, such as the anatomy or biology of the species that the fossils represent; (2) the taphonomic processes, both biological and physical; and (3) the fossil assemblage in its sedimentary context. For both loss and gain approaches, the fossil assemblage provides the evidence. The difference between the two approaches lies in which building block is treated as the unknown of interest (the subject of investigation), and which is treated as an assumption (for example, the conclusions of a prior study). In the loss approach, the living community is the unknown of interest, for the purpose is to reconstruct some aspect of the original community, while the taphonomic processes are assumed. In the gain approach, the taphonomic processes are the unknown of interest, because recognizing the action of a process leads to new information about the environment. However, the

process can only be recognized if its starting point (the original condition of the community or organisms) can be assumed (Figure 12).

The fact that loss and gain approaches must make assumptions in the area of each others' conclusions means that although they can complement each other, there is also some danger of conflict (Figure 12). If loss-oriented taphonomists assume aspects of taphonomic processes that have been well tested by gain-oriented studies, and conversely, if gain-oriented taphonomists assume aspects of living communities that have been well tested by loss-oriented studies, both approaches can make more reliable advances. In accepting the conclusions of the opposite approach, the assumptions that led to those conclusions are implicitly accepted as well. Obviously, there is some danger of circularity, and the network of interconnecting assumptions and conclusions can become very complex.

In both loss and gain approaches, the assumptions are often the weakest link. Many of the assumptions made in taphonomy are uniformitarian in nature. Some authors distinguish between "methodological" and "substantive" uniformitarianism in historical science (Valentine, 1973), with the former referring to timeless physical and chemical properties and processes, and the latter referring to uniformity of rate and intensity of processes over time. "Methodological" uniformitarianism is true of all scientific inquiry, whereas "substantive" uniformitarianism, strictly interpreted, is not valid. We proceed, therefore, by distinguishing among "substantive" uniformitarian assumptions, choosing those likely to have changed the least.

Three of the most common assumptions made by taphonomists are: (1) Similar taphonomic characteristics in fossil assemblages are caused by similar processes. (2) The physical and biological taphonomic processes that operated in the past are similar to the processes that operate today. (3) Original conditions, such as anatomy, community structures, and population characteristics, are similar to those of today. These assumptions are most likely to be reliable if they concern physical conditions and processes. However, they are more likely to be untrustworthy if they concern biological ones, because organisms are continually evolving, and extrapolations are often being made over long periods of geologic time. For example, in loss-oriented studies, assumptions about the existence and intensity of biological processes such as predation, scavenging, and decay are particularly suspect. In gain-oriented studies, assumptions about biological aspects of the living community such as population characteristics are suspect for the same reason.

However, the situation is not hopeless even for biological assumptions. Some bio-

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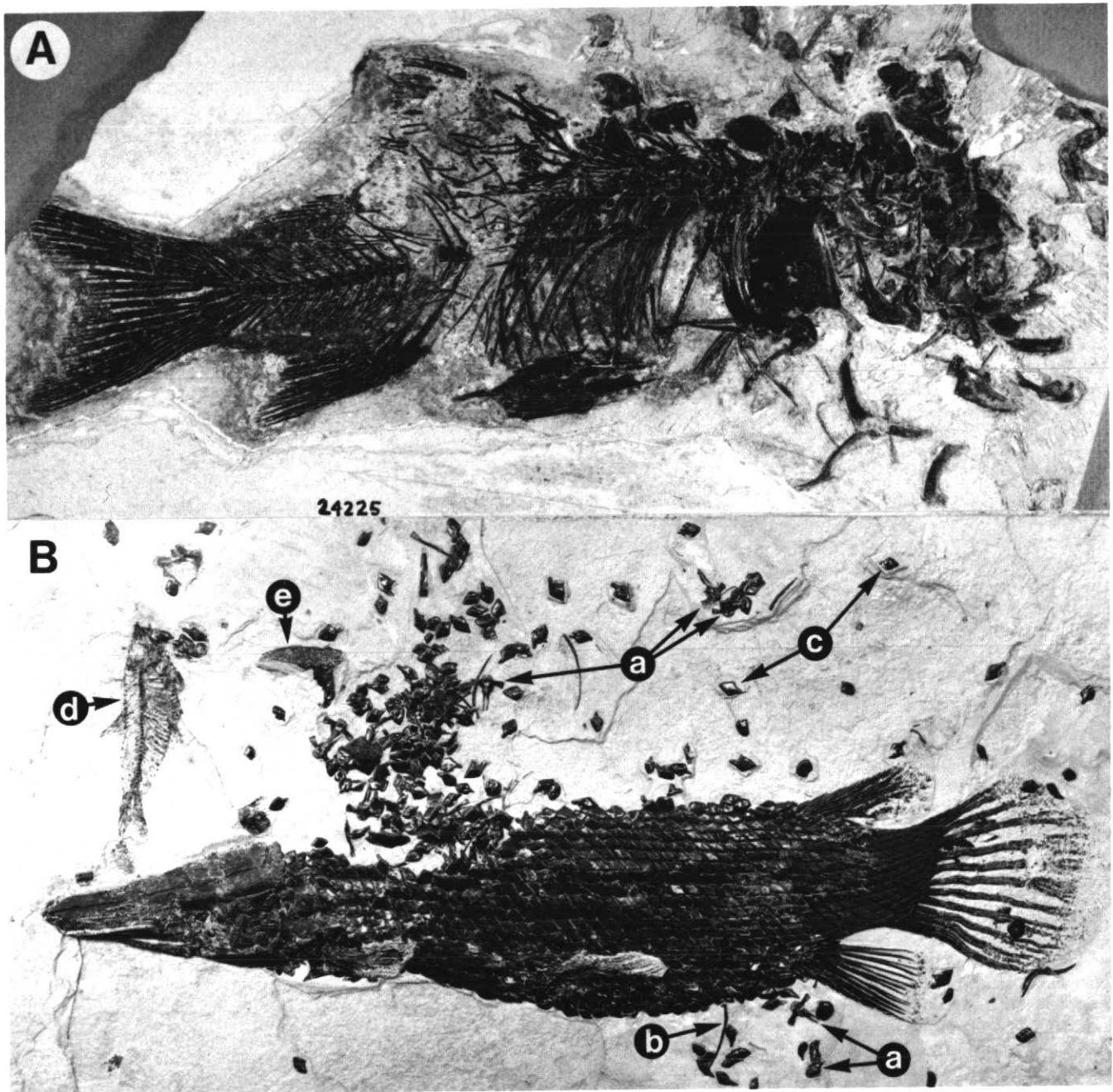
Figure 10 *Displacement of bones from partly disarticulated fish skeletons is a source of taphonomic gain about physical and biological conditions in lakes.*
(A) *The catostomid fish Amyzon aggregatum in varved lacustrine sediments of the Eocene Horsefly beds, British Columbia. Most of the fossil fish in this deposit are preserved with little or no disarticulation (Wilson, 1984), but this fish shows characteristics of skeletons disarticulated by scavengers. In Elder's (1985) experiments, scavenged skeletons usually had bones displaced in random directions mostly from the skull. Scavenging in turn implies that oxygenated water was present in this spot during at least part of the year.*
 (B) *The gar Atractosteus simplex in lacustrine marls of the Eocene Green River Formation, Wyoming, USA, photo courtesy of L.A. Lindoe. This fish shows characteristics of explosive release of decay products from the body cavity under conditions of very gentle currents. There is no evidence of either scavenging or disarticulation by turbulence, but it is likely that decay within the body cavity produced a soupy mixture that included vertebrae and ribs. The built-up pressure was released by failure of the body wall near the right pectoral fin, causing scales, vertebrae, and ribs to flow toward the top of the photo, with some of the bones and scales carried by very gentle water movements toward the bottom of the photo.* **(a)** *gar vertebrae;* **(b)** *rib;* **(c)** *gar scales;* **(d)** *a small fish, Diplomystus sp.;* **(e)** *gar preopercular bone.*
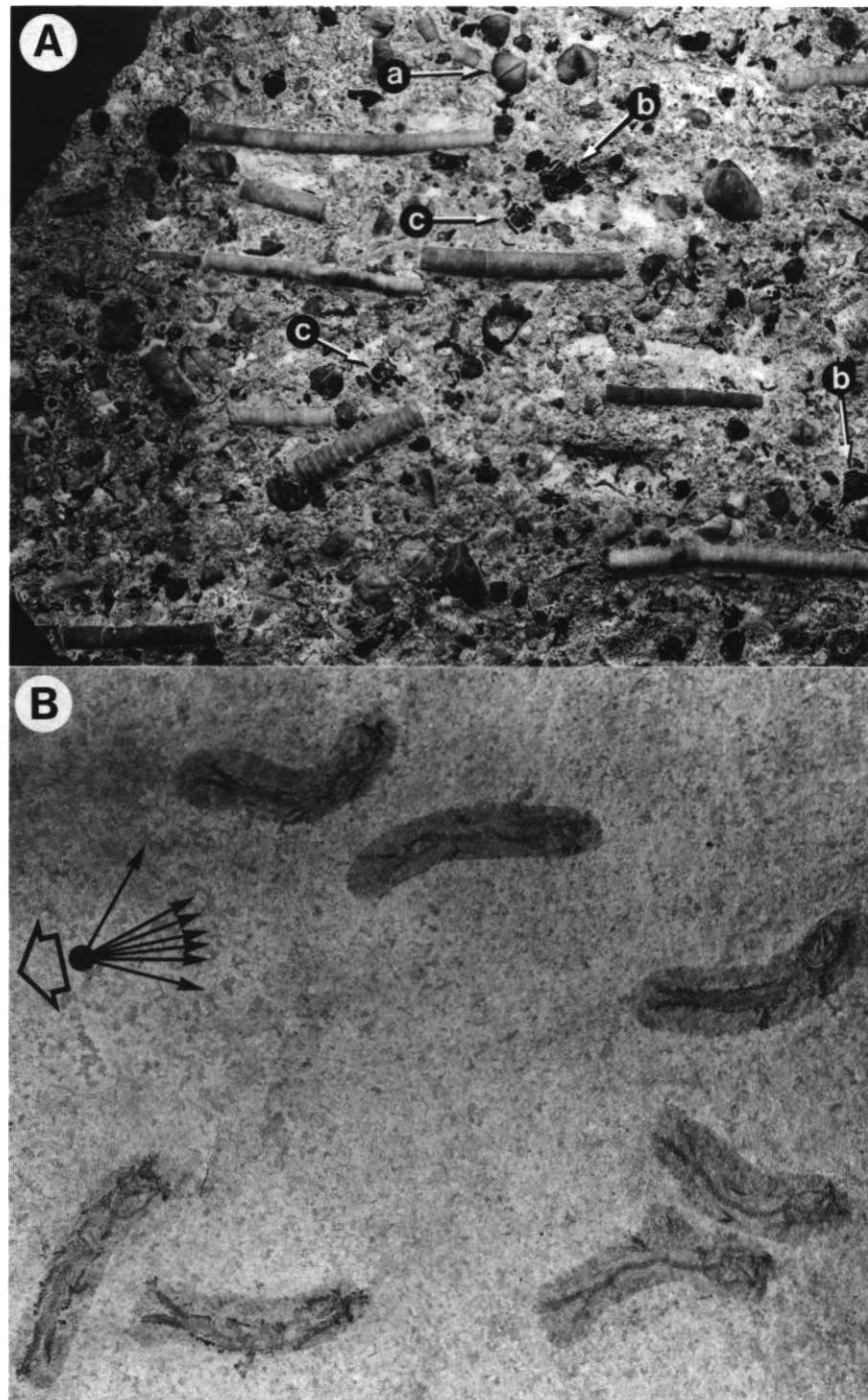
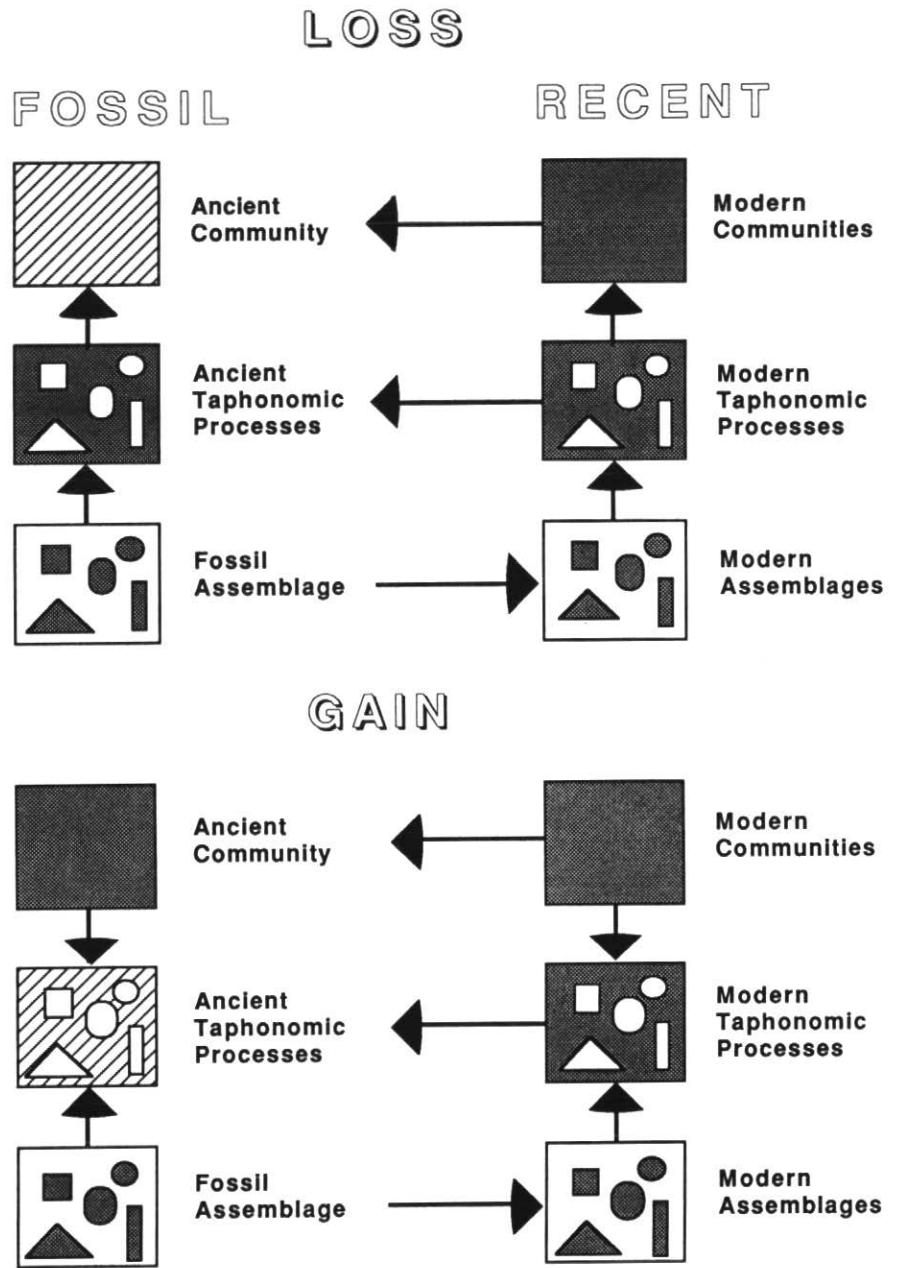**Figure 11** *Orientation of fossils by currents or waves.*

(A) *As with Figure 9, this slab from the Lower Silurian Jupiter Formation of Anticosti Island may record more than one taphonomic régime. The matrix of fragmented skeletal remains, including many disarticulated crinoid elements with some larger pieces of brachiopods and trilobites, likely represents a significant amount of time during which turbulence and/or currents reduced most fossils to small fragments. Subsequently, large, articulated segments of crinoid stems became aligned by a fairly gentle current flowing either from left to right or from right to left in the photo (alternatively, the alignment could have been caused by waves running from top to bottom or from bottom to top in the photo).   **(a)** brachiopod (Pentamerus sp.);   **(b)** pygidia of trilobites (Dystrax sp.);   **(c)** cephalons of trilobites (Calymene sp.; note that these are not the same species as the pygidia which are most abundant on this slab).*

(B) *Seven small specimens of the fish* Leptolepis sprattiformis *from the Upper Jurassic Solnhofen Lithographic Limestones (a Fossil-Lagerstätten) of southern Germany. Lack of disarticulation, the small size of the fish, and the fine grain of the sediment suggest a very low current velocity, perhaps a convection current in what is thought to be a lagoon-like body of water. The fish also show typical effects of anoxia (arched vertebral column, wide-open mouth), suggesting that they may have died of suffocation. Unlike the crinoid stems in* **A***, which do not discriminate between the two opposite possible current directions, the fish are oriented with their heads pointing approximately into the current. Each of the small black arrows shows the orientation of one of the seven fish; the large broad arrow shows the inferred current direction, oriented 180 degrees from the average orientation of the seven fish. Much larger slabs containing hundreds and thousands of oriented fish like these have been found at Solnhofen.*

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Figure 12 *The assumptions and logic of taphonomic loss and taphonomic gain. Large shaded boxes represent evidence and assumptions, including conclusions from previous studies. Large cross-hatched boxes represent the particular hypothesis that is being tested by new observations. The process boxes contain white openings, which represent the selective "templates" of the taphonomic process, through which some but not all organic remains pass and are modified. The assemblage boxes contain shaded objects which represent the resulting selected, modified remains. The arrows represent the directions of the inferences.*

LOSS: In order to test an hypothesis about the ancient community, such as its faunal composition or some life-history characteristic of one of its species (hatched ancient-community box), the existence or intensity of ancient taphonomic biases must be assumed (ancient-process box). The logic of taphonomic loss also often involves Recent analogies (horizontal arrows). As an example, seasonal reproduction of a species (hatched box) might be inferred from a polymodal size distribution (fossil-assemblage box), as with Recent organisms. However, this inference assumes that there is independent evidence (for example from preservation on a single bedding plane, from sedimentology, or from other fossils) that death of all the fossils was nearly simultaneous (ancient-process box). [Polymodal size distributions could also be caused by non-simultaneous age-selective mortality.] Existence of a polymodal size distribution in the assemblage cannot also be used to support the conclusion that death was simultaneous, because simultaneous death was assumed when the size distribution was used to infer seasonal reproduction.

GAIN: In order to test an hypothesis about the existence or intensity of a taphonomic process, such as cause of death or selective removal of small size classes by dissolution (hatched ancient-process box), the pre-existing condition must be assumed (shaded ancient-community box). This condition in turn is often assumed to be similar to Recent examples (horizontal arrow from Recent-community box). As an example, the existence of a polymodal size distribution in the fossil assemblage (fossil-assemblage box) might be taken as evidence of simultaneous ("catastrophic") death, as is often the case with Recent organisms. However, this argument assumes (for example from existence of annuli on shells or bones, or from Recent analogies) that reproduction in the organism was seasonal (shaded ancient-community box). The existence of a polymodal size distribution cannot also be used to support the conclusion that reproduction was seasonal, because seasonal reproduction was assumed when size distribution was used to infer simultaneous death.

LOSS

FOSSIL   RECENT

Ancient Community — Modern Communities

Ancient Taphonomic Processes — Modern Taphonomic Processes

Fossil Assemblage — Modern Assemblages

GAIN

Ancient Community — Modern Communities

Ancient Taphonomic Processes — Modern Taphonomic Processes

Fossil Assemblage — Modern Assemblages

reliable independent fossil evidence. As a simple example, even though there are no extant trilobites we can safely assume that 400 million-year-old trilobites had an articulated cephalon, thoracic segments, and pygidium, because there are many examples of fully articulated specimens of about the same geologic age as the disarticulated specimens under study (Figure 3).

Loss-oriented taphonomists seem to have avoided some of the pitfalls of biological assumptions by emphasizing assumptions about physical processes of taphonomic loss, such as hydrodynamic and chemical behaviour of skeletal remains (although usually they must still assume certain biological aspects of the original community). Gain-oriented taphonomists might similarly emphasize assumptions about physical aspects of the original community, using the model of gain-oriented sedimentology, unless they are extrapolating their assumptions over short periods of geologic time or have strong independent evidence for biological aspects of the community.

Are all three common assumptions (see above) necessary for both loss and gain taphonomy? The first assumption seems to be necessary for both schools (Figure 12), as it is for much of biology and geology. However, the second and third assumptions, particularly as they relate to biological phenomena, are not always necessary. If they were, then loss-oriented taphonomists could never reconstruct community structures that differ from ones existing today. Similarly, gain-oriented taphonomists could never postulate processes different from those operating today. The most radical finding that could be hoped for is that communities and processes have changed in distribution and proportion, but not in kind. We can keep open the possibility that communities and biological processes have changed by emphasizing the physical assumptions, or those biological assumptions for which independent fossil evidence exists.

Laws, Principles, or Generalizations about Burial
In his review of the field of taphonomy, Olson (1980) decried the absence of a set of principles or "laws" of burial, and he was not particularly optimistic that generalizations across taxonomic or geologic boundaries would be easy. Have recent developments in taphonomy furthered the development of such "laws" — or should we expect them to do so?

Strictly speaking, a search for "laws" is inappropriate, even though the concept of "laws" was included by Efremov (1940) when he coined the word "taphonomy". Neither biology nor geology has a body of laws of its own; these fields are themselves synthetic mixtures that depend upon the laws of physics and chemistry. The highest level of scientific generalizations that have been

applied to biology and geology are usually called theories (e.g., evolution, plate tectonics). Therefore, taphonomy, which mixes paleontology with sedimentary geology, is unlikely to have laws apart from those of physics and chemistry, or even theories that are not also theories of biology, paleontology, geology, and/or sedimentology. Perhaps, as Olson (1980) hinted, we should be asking whether or not there are broadly applicable generalizations in taphonomy, such as principles, hypotheses, or models, that have explanatory power concerning the process of fossilization.

Supposing that taphonomists do find meaningful principles, hypotheses, or models of fossilization, will anyone besides taphonomists need or use them? Paleoecologists, evolutionary biologists, biostratigraphers, and systematists might be interested particularly in loss-oriented generalizations. Sedimentologists and paleoecologists might be able to use gain-oriented generalizations. However, as Gould (1980) and Olson (1980) suggested, meaningful generalizations are more likely to be found if taphonomy breaks away from narrow restrictions of taxonomy and habitat, as it seems to be doing increasingly today.

Some of the generalizations that have been discussed in this paper are preliminary in nature and still in need of further testing. Nevertheless, they represent a first step, and are summarized below.

Some Generalizations about Burial from Recent Studies
1. Disarticulation, alteration, and destruction, as a result of predation, scavenging, decay, dissolution, transportation, and abrasion lead to loss of information, including diversity, between the community and the fossil assemblage. However, gain in knowledge about the ancient environment can result from recognition of the characteristic effects of these taphonomic agents.

2. Transportation, reworking, tiering, and lag deposits lead to spatial and temporal mixing and thus to potential confusion between communities. Temporal mixing is a problem in many fossil concentrations, but is often unrecognized.

3. Absence of decay, scavenging, and turbulence, as well as rapid burial, can lead to exceptionally good preservation of specimens.

4. Taphonomic loss is severe in shallow marine habitats; usually less than half the diversity is preserved.

5. For marine and lacustrine organisms, destruction, particularly of small size classes, accounts for more taphonomic loss than transportation or spatial mixing.

6. For terrestrial vertebrates and plants, and for fluvial organisms, transportation causes much taphonomic loss in the form of disarticulation, selective destruction, sorting, and mixing.

7. Temporal mixing leads to falsely increased variability of morphological features in samples from changing populations such as evolving lineages. Spatial mixing similarly leads to increased variability in samples from geographically-variable species.

8. The more temporal mixing there is, the fewer population features can be reconstructed, because population features often vary over short temporal intervals. Mass-death layers are thus usually more useful than attritional-death layers for reconstructing certain population characteristics. Multiple mass-death layers are even better, for they can record temporal variability of the population characteristics.

9. In biostratigraphy, false late appearance and false early extinction are common results of taphonomic loss. False late extinction and false early appearance also occur, but, of these two, false late extinction is the more common and severe.

Summary
Taphonomy is a new and growing field of interest to paleoecologists, evolutionary biologists, biostratigraphers, systematists, and sedimentologists. Its definition and scope are still being debated. There are two approaches in taphonomic work, one emphasizing the negative effects of the death and burial processes upon research goals (taphonomic loss), and one emphasizing the potential positive effects (taphonomic gain). The two approaches can be complementary. In both approaches, the assumptions can be the weakest link and the researcher must take care to ensure that they are both reliable and necessary. Generalizations about fossilization can be drawn that are of relevance to biology and geology in general.

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